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Spatial and temporal variation in community composition of herbivorous insects on *Neoboutonia macrocalyx* in a primary tropical rain forest

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Abstract: Spatial and temporal variation of tropical insect communities has rarely been studied, although such variation influences estimates of global species richness. Therefore, we compared spatial and temporal variation of herbivorous insect communities on *Neoboutonia macrocalyx* trees among seven sites over 1 y in a primary tropical rain forest in Kibale National Park, Uganda. The distance between the study sites varied from 4.8 to 31.2 km and altitudinal differences ranged from 20 to 242 m. Permutational multivariate analysis of variance (PERMANOVA) revealed significant spatial changes in community composition of the herbivorous insects and study sites differed also in insect abundance (6.9–26.2 individuals m^{-2} of leaf area). This is likely to be caused by differences in vegetation, altitude and microclimate among the study sites. The similarity of insect species composition was negatively correlated with geographic and altitudinal distances among sites and positively correlated with the similarity of tree community composition. Species richness varied significantly between sampling dates, ranging from 33 to 41 species. Also community compositions changed between sampling dates, which likely follows from marked seasonal changes in climate and the phenology of other host plants used by the generalist insect species also living on *Neoboutonia macrocalyx*. In general our study supports the idea of high variability of herbivorous insect communities in primary rain forests even at a small spatial scale. This should be considered when estimations of insect biodiversity are made.

Key Words: Afrotropical rain forest, insect communities, Kibale National Park, *Neoboutonia macrocalyx*, species composition, Uganda

INTRODUCTION

The number of described and named insect species is over 900 000 but a large part of the total insect species has not yet been discovered (Price 2002). Estimates of global insect species range from 30 million (Erwin 1982) to a more recent 4–10 million species (Basset *et al.* 1996, Novotny *et al.* 2002a, Ødegaard *et al.* 2000, Thomas 1990). In order to better estimate the global number of insect species, inventories should be made at several sites inside a given region during at least 1 y, because insect communities can vary spatially and temporally (Erwin *et al.* 2005, Molleman *et al.* 2006). However, few studies have analysed spatial and temporal variability in community composition of tropical herbivorous insects (Brehm *et al.* 2003).

Because of the latitudinal increase in species richness towards the equator and a latitudinal decrease in species' range of distribution (Rapoport's rule), spatial species turnover in the tropics should be high (Rosenzweig 1995, Stevens 1989). Dyer *et al.* (2007) found turnover in species composition of Lepidoptera in tropical forests in South America. However, in several studies in tropical rain forests, the local species pool represents a large proportion of the regional insect community (Bartlett *et al.* 1999, Gaston & Gauld 1993). In these cases, the alpha diversity is higher than the species turnover. Little change in species composition of herbivorous insects was also found in tropical lowland rain forest in Papua New Guinea by Novotny *et al.* (2007). Novotny & Weiblen (2005) suggest that species turnover around the equator is low because most insect species are specialized on plant genera and families rather than on single species, and many species-rich plant genera are widely distributed (Condit *et al.* 2002, Novotny *et al.* 2002b, Pitman *et al.* 1999). The same kind of high alpha diversity and low species turnover is common in tropical tree species (Kochummen *et al.* 1992). On the other hand, in studies of compositional

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variation, the proportion of rare species may have been underestimated (Erwin 1991).

The purpose of this study is to explore the extent of spatial and temporal variation in community composition of herbivorous insects at seven primary tropical rainforest areas on five sampling dates during 1 y in Kibale National Park, Uganda. We use a locally abundant tree species, *Neoboutonia macrocalyx* Pax, and its associated insect community as our model system. We hypothesize that spatial variation in community composition is low because the study sites represent relatively homogeneous primary rain forest, and because *N. macrocalyx* produces leaves around the year (Kasenene & Roininen 1999). Furthermore, Kibale National Park constitutes a quite small and isolated habitat. By contrast, temporal variation in community composition is hypothesized to be high due to marked variation in temperature, precipitation and resource competition throughout the year (Savilaakso *et al.* 2009, Skippari *et al.* 2009).

METHODS

Study area

The study was conducted from April 2008 to April 2009 in Kibale National Park (766 km^2) located in Western Uganda (0°13′–0°41′N, 30°19′–30°32′E) (Struhsaker 1997). The area represents moist transitional forest between lowland tropical forest and montane forest (Struhsaker 1975). The park contains various habitats including mature forest, secondary forest, swamp, grassland and woodland thicket. The altitude changes from about 1590 m asl in the northern parts of the park to 1110 m asl in the southern parts (Struhsaker 1997). The mean annual rainfall was 1749 mm during 1990–2001 and the area has two rainy seasons, the first from March to May, and the second from October to December (Chapman *et al.* 2005). Mean daily temperatures during 1990–2001 ranged between 14.9 °C and 20.2 °C.

Study tree

Neoboutonia macrocalyx Pax grows in gaps of medium-altitude rain forests, in moist areas, and in valley bottoms in central and eastern parts of tropical Africa (Chapman *et al.* 1999, Lovett *et al.* 2006). *Neoboutonia macrocalyx* is a pioneer tree, which colonizes gaps and disappears when the gaps close during forest succession. It is common especially in partly logged secondary forests (Kasenene & Roininen 1999). The trees are 10–20 m tall and the canopy width is typically 7–12 m (Hamilton 1991). *Neoboutonia macrocalyx* is one of the 20 most common tree species in Kibale National Park (Cords 1990). It produces new leaves throughout the year, so access to food should not limit the abundance of insect herbivores on the plant (Kasenene & Roininen 1999).

Insect sampling

Seven primary-forest areas were selected for this study: Sebitoli (0°37′24.00″N, 30°24′18.00″E), Compartment K30 (0°33′27.24″N, 30°21′31.26″E), Mpanga River (0°33′58.50″N, 30°28′58.80″E), Machwamba River (0°31′36.18″N, 30°23′22.20″E), Ngogo (0°29′39.48″N, 30°25′29.52″E), Dura River (0°27′30.84″N, 30°22′47.58″E) and Mainaro (0°21′34.02″N, 30°23′17.76″E). The size of the sampling sites varied from 4.7 to 19 ha when measured with 50-m radius around the outermost sampled trees. The distances between sites varied from 4.8 km to 31.2 km, and altitudinal differences ranged from 20 to 242 m.

From each site, insect community samples were collected five times: The first, 22 April–21 May 2008; the second, 9 July–23 July 2008; the third, 15 September–2 October 2008; the fourth, 6 November–25 November 2008; and the fifth, 29 March–7 April 2009. Hereafter, the sampling dates will be referred to by the starting month of the sampling. During each sampling, 20 *N. macrocalyx* trees were chosen randomly from each area, and six random branches were cut from each tree using tree pruners. The branches were cut from the lower parts of the canopy at 6–13 m height, and dropped down to a 4-m^2 sheet under the tree. All insect larvae observed to feed on leaves were collected from the branches, and then stored in 95% ethanol. Also the galls and mines on the leaves and tunnels caused by a petiole-boring Curculionidae species were counted.

The sampled larvae were separated into morphospecies and counted. For lepidopteran larvae, family- and genus-level identifications of most morphospecies were confirmed by sequencing the standard 658-bp DNA barcode region of the mitochondrial COI gene (Hebert *et al.* 2003) from a subset of the sampled larvae (1–8 individuals per morphospecies) using standard protocols. In order to check that larval morphospecies grouped together as single species, we constructed a neighbour-joining tree of the samples based on Kimura 2-parameter distances in Mega version 5 (Tamura *et al.* 2011). Working names for morphospecies were given based on the identification tool of the BOLD barcode database (Ratnasingham & Hebert 2007) (Appendix 1). COI barcode sequences of these samples have been submitted to GenBank under accession numbers KC172703–KC172825. A total of 299 (2.1% of the total sample) individuals belonging to the lepidopteran families Geometridae, Erebidae, Gelechiidae, Oecophoridae, Pyralidae, Psychidae and Noctuidae were excluded from further community analyses, because we were not able

to reliably classify them by morphological characters and/or because barcoding of the putative morphogroups indicated that they did not constitute species units.

The number of herbivore individuals per morphospecies was divided by the total leaf area in each sample, in order to standardize insect density with respect to sample sizes. For this, the midribs of all leaves from cut branches were measured in order to estimate the leaf area, which can be calculated using the formula $Y = 5.03x + 0.83x^2$, where x is the midrib length and Y is the leaf area (Savilaakso *et al*. 2009).

Tree community

The area for the study of tree community was determined as a matrix of 50-m around the outermost sampled trees of *N. macrocalyx* at each site. Ten sampling plots (20 × 20 m) were randomly set inside the determined area. All trees having a diameter of at least 10 cm at breast height ($dbh_{1.3}$) were sampled and identified to species or in a few cases only to genus (Appendix 2). The summed cross-sectional area of each tree species at breast height was used as a measure of abundance in analyses of tree community composition.

Data analyses

Accumulation curves of insect species richness at each site and at all sites combined were estimated by EstimateS (version 8.0, R. K. Colwell, http://purl.oclc.org/estimates). Simpson's diversity index and Berger–Parker dominance index were calculated for every study site during each sampling date with Species Diversity and Richness (version 4.0, Pisces Conservation Ltd, Lymington, UK), and the averages were used as a measure of total alpha diversity of each site. Species richness with 95% confidence intervals was estimated using sample-based rarefaction in EstimateS as proposed by Gotelli & Colwell (2001), because the number of insect individuals differed among samples. To test the hypotheses that sampling site and/or date affect the alpha diversity indices (species richness, Simpson's diversity index and Berger–Parker dominance index) and/or the density of the insects, multivariate analysis of variance (MANOVA) was conducted using log-transformed data, while using site as a fixed factor and dates as covariates, and vice versa. If the MANOVA indicated significant differences between sites or dates, univariate analysis of variance (ANOVA) was performed for each variable.

The number of shared insect species between sites was calculated using Species Diversity and Richness. In order to estimate the pairwise similarity of sampling sites in percentages, the Bray–Curtis similarity index was calculated with PRIMER (version 6, PRIMER-E Ltd, Plymouth). For this, the density data were fourth-root transformed to reduce the effect of the most common species, and a dummy variable of one was added because of the many zero observations (Clarke & Gorley 2006). Non-metric multi-dimensional scaling (NMDS, 50 restarts) in PRIMER was used to represent the sampling sites across five sampling times and the five sampling times across seven sampling sites in two-dimensional ordination space. NMDS seeks an ordination in which the distances between the points in ordination space are in the same rank order as their similarities in species composition, in our case Bray–Curtis similarity. Distances among centroids of sampling sites and dates were used. The stress value measures how well NMDS fitted the multidimensional data into two-dimensional space.

Transformed Bray–Curtis similarity data were also used for permutational multivariate analysis of variance (PERMANOVA) in PRIMER, which was used to test for differences in composition of insect species among different sampling sites and dates. Main tests were conducted across two random factors, and 9999 unrestricted permutations were performed. The same tests were applied for tree-abundance data with the same transformations and similarity measures as for the insect density data, except that only the effect of study site was tested. To find the insect species that contributed most to the observed differences among sites, a similarity percentage (SIMPER) analysis was performed on fourth-root-transformed density data with PRIMER.

Finally, Mantel tests in PC-ORD (version 5.0, MjM Software, Gleneden Beach) were used to test for correlations between the similarity of insect community structure, the similarity of tree community composition, geographical distances and altitudinal differences among sites. Significances are based on 9999 randomizations.

RESULTS

In total, 14 024 individuals representing 63 insect herbivore species were captured. The average insect density was 16.2 individuals m^{-2} of leaves. The species represented four orders: Lepidoptera, Diptera, Hemiptera and Coleoptera. The most common morphospecies were Cecidomyiidae sp. 2 (the hard leaf gall), Microlepidoptera sp. 1 (the round miner) and Geometridae sp. 1, which altogether represented 83% of all individuals. Out of all species, 24% were represented by only one individual, and 9% were represented by two individuals. The highest number of individuals was found from Machwamba River (2901) and lowest from Dura River (1015) (Table 1). Out of all sampling months, the number of individuals was highest in March (3815) and lowest in November (1773) (Table 2). The species-accumulation curve did not reach an asymptote when all sites were pooled (Figure 1).

Table 1. Abundance, species richness, density (± SE), Simpson's D (± SE) and Berger–Parker Dominance index (± SE) of insect communities on *Neoboutonia macrocalyx* for the seven study sites in Kibale National Park.

Site	Abund. (N)	Species richness (95% CIs)	Density (inds. m^{-2})	Simpson's D	Berger–Parker
Sebitoli	2598	36.6 (29–44)	20.6 ± 4.5	3.03 ± 0.35	0.51 ± 0.05
Compartment K30	2670	36.9 (29–45)	20.2 ± 4.2	3.00 ± 0.30	0.49 ± 0.04
Mpanga River	2209	35.0 (28–43)	15.5 ± 7.7	1.93 ± 0.60	0.77 ± 0.10
Machwamba River	2901	37.8 (30–45)	27.1 ± 4.0	2.96 ± 0.84	0.56 ± 0.07
Ngogo	1384	30.6 (23–38)	10.9 ± 2.9	2.51 ± 0.39	0.60 ± 0.08
Dura River	1015	27.6 (20–35)	6.6 ± 1.2	2.88 ± 0.13	0.53 ± 0.03
Mainaro	1247	29.6 (22–37)	10.9 ± 1.5	3.78 ± 0.55	0.41 ± 0.06

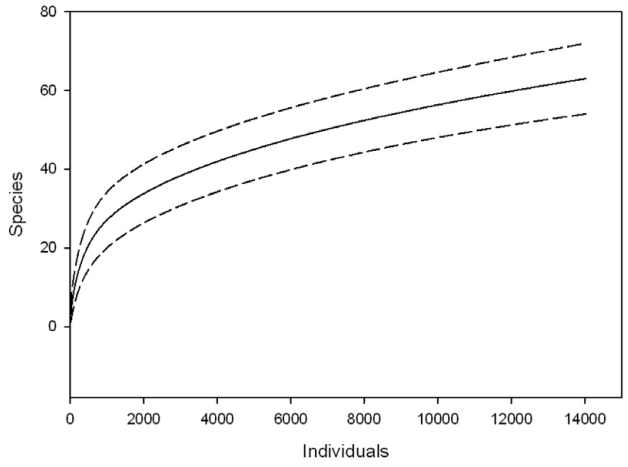

Figure 1. Species-accumulation curve of the herbivorous insects on *Neoboutonia macrocalyx* in Kibale National Park with 95% confidence intervals for all sites pooled.

The overall effect of sampling site on alpha diversity indices and density of insects was statistically significant (MANOVA; $F_{(24, 85)} = 1.85$, P = 0.02; Wilks' Lambda = 0.23; Table 1). This was caused by the density of the insects, which varied among sampling sites (ANOVA; $F_{(7, 35)} = 3.85$, P = 0.007), while species richness, Simpson's D and Berger–Parker dominance index did not differ significantly among sites (ANOVA; $F_{(7, 35)} = 2.08$, P = 0.089; $F_{(7, 35)} = 2.18$, P = 0.076; $F_{(7, 35)} = 2.34$, P = 0.06, respectively). The overall effect of sampling date on alpha diversity indices and density of insects was also significant (MANOVA; $F_{(16, 80)} = 4.22$, P < 0.001; Wilks' Lambda = 0.16; Table 2). This was caused by species richness, which varied among the sampling dates (ANOVA; $F_{(5, 35)} = 3.51$, P = 0.019), while the density of insects, Simpson's D and Berger–Parker dominance index did not differ significantly among dates (ANOVA; $F_{(5, 35)} = 0.57$, P = 0.690; $F_{(5, 35)} = 1.38$, P = 0.267; $F_{(5, 35)} = 1.00$, P = 0.424, respectively).

Table 3. PERMANOVA main tests for differences in community composition of herbivorous insects on *Neoboutonia macrocalyx* among sampling sites, sampling dates and the interaction between sites and dates in Kibale National Park. Degrees of freedom (df), Pseudo F-value (Pseudo-*F*), permutational p-value (P), unique values of the test statistic obtained under 9999 permutations (Unique perms) and estimated components of variation are shown.

	df	Pseudo-*F*	P	Unique perms	Estimated components of variation
Sampling site	6	5.72	0.0001	9910	16.1 (14.7%)
Sampling date	4	4.71	0.0001	9918	12.1 (8.3%)
Site × date	24	4.51	0.0001	9779	14.6 (12.1%)

The composition of insect communities differed significantly among the sampling sites and dates (Table 3, Figure 2a, b). There was also a statistically significant interaction between sites and collection dates. Compartment K30 and Sebitoli had the highest number of shared insect species (29), while Mainaro and Ngogo had the least (16). Based on the sampling dates, March and April, and March and November, had the highest number of shared species, while July and November had the least. The species that contributed most to the differences between the forest sites were also the most abundant species: Cecidomyiidae sp. 2 (hard leaf gall), Microlepidoptera sp. 1 (round miner), Geometridae sp. 1 and Curculionidae sp. 1 (petiole borer, adult). Also the tree community composition differed significantly between sampling sites (Permanova; pseudo-F = 3.59, P = 0.0001).

Table 2. Abundance, species richness, density (± SE), Simpson's D (± SE) and Berger–Parker Dominance index (± SE) of insect communities on *Neoboutonia macrocalyx* for the five sampling dates in Kibale National Park.

Date	Abund. (N)	Species richness (95% CIs)	Density (ind. m^{-2})	Simpson's D	Berger–Parker
April 2008	2958	38.0 (31–46)	17.8 ± 4.5	2.74 ± 0.33	0.56 ± 0.06
July 2008	3233	39.0 (32–47)	18.9 ± 5.5	2.11 ± 0.25	0.65 ± 0.07
September 2008	2245	35.2 (28–43)	13.7 ± 2.7	3.35 ± 0.42	0.48 ± 0.05
November 2008	1773	32.9 (25–40)	11.0 ± 2.5	2.82 ± 0.38	0.55 ± 0.06
March 2009	3815	41.1 (33–49)	18.5 ± 4.8	3.32 ± 0.63	0.53 ± 0.08

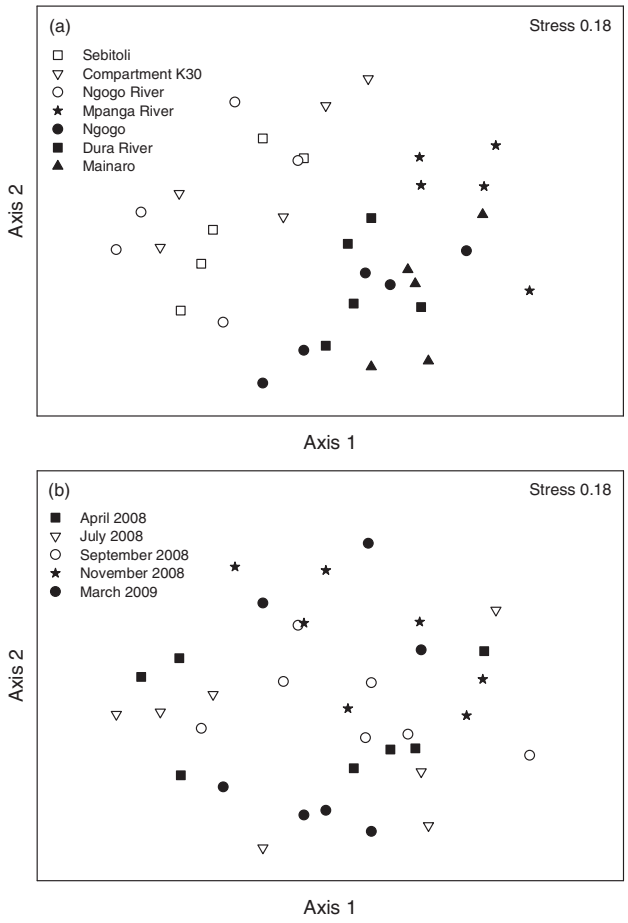

Figure 2. Non-metric multidimensional scaling ordination of the seven study sites during five sampling times (a) and the five sampling times at seven study sites (b) based on their herbivorous insect communities on *Neoboutonia macrocalyx* in Kibale National Park. Distances among centroids of sampling sites and dates were used. The stress value indicates that the ordination is a fairly good representation of the data.

Faunal and floristic similarity, distance among sites and altitudinal differences among sites correlated with each other. The similarity of insect community composition correlated positively with similarity of tree communities (Mantel test, $r = 0.54$, $P = 0.03$). Insect community similarity was negatively correlated with both geographic distance and altitudinal separation (Mantel test, $r = -0.60$, $P = 0.03$; Mantel test, $r = -0.50$, $P = 0.02$). Geographic distances and altitudinal differences among the sites correlated also significantly (Mantel test, $r = 0.61$, $P = 0.005$).

DISCUSSION

Spatial variation in community composition

We found considerable change in community composition of herbivorous insects in a tropical rain forest, despite the fact that the maximum distance between our study sites was only 31.2 km. The greater the difference in distance or altitude was between study sites, the more their community compositions differed. This is most likely a typical phenomenon for medium-altitude rain forests, since the landscape is a combination of hills and river valleys that cause isolation among patchy populations of tree species such as *N. macrocalyx*. Few studies of variation in insect community composition have been made in tropical areas that are assumed to be environmentally relatively homogeneous. In a beetle study conducted in Venezuelan rain forest, the community composition changed between sites 20 km apart (Davies *et al.* 1997). Spatial turnover was also high among caterpillars in other South American rain forests (Dyer *et al.* 2007). Like ours, these studies contradict the hypothesis of low spatial change in tropical rain-forest insect communities suggested by Novotny *et al.* (2007). In their study on Papua New Guinean insect communities, they found that among-site variation in species composition in caterpillars (Lepidoptera), ambrosia beetles (Coleoptera) and fruit flies (Diptera) was low even up to distances of 500 km. Likewise, weevils in the Western Amazon Basin show low species turnover when distance between study sites was 21 km (Erwin *et al.* 2005). In a study on Bornean butterfly communities, Cleary & Genner (2006) found that community similarity decreased with geographical distance over small distances (< 2 km), but increasing inter-site distances led to only minor changes in mean similarities. Only 43–60% of all the species found in this study were present at one study site when the whole year sampling was considered. This is less than what Basset *et al.* (2012) estimated in Panama where over 60% of all local insect species were assumed to be present in 1 ha of rain forest. However, all the aforementioned studies have been performed on multiple host plants whereas in our study only one host species was considered.

Although our study sites were selected from seemingly uniform primary rain forest, we found clear local differences in tree community composition. Also Chapman *et al.* (1997) found variation in vegetation between the southern and northern parts of Kibale National Park. Differences in plant communities can influence the community structure of herbivorous insects (Crist *et al.* 2006, Savilaakso *et al.* 2009, Summerville & Crist 2003, Whitham *et al.* 2006). Herbivorous insects are entirely dependent on plants as nutrition, and differences in plant species composition change the insect species composition especially when there are generalist species. Generalists can use different host species and move to *N. macrocalyx* or away from it according to the phenology of other available hosts.

Intercorrelated biotic (similarities in insect and tree communities) and abiotic (geographic and altitudinal distances) factors make evaluation of causal factors underlying observed spatial variation in insect communities

difficult. In our study, community composition was linked to altitudinal differences among sites despite the fact that maximum differences in altitude were minor (< 242 m). Sebitoli and Mainaro differed the most in elevation, but at the same time they were also located the furthest away from each other. These two places also differed greatly in their insect species composition. Because the elevational and geographic distance correlated, it is hard to determine the factor that most affects the change in insect assemblages. We would emphasize the influence of elevation, because it has an effect on both climate and vegetation of the Kibale National Park. Even small changes in the microclimate, e.g. temperature or humidity, can influence insect communities (Basset 1991, Intachat *et al.* 2001, Savilaakso 2009). In Kibale, the climate is relatively stable but the microclimate can vary locally (Savilaakso *et al.* 2009). Chapman *et al.* (1997) found that in Kibale National Park average temperatures rise and precipitation decreases from north to south. Local climate changes also temporally, mostly because of unpredictable timing of the rainy seasons (Chapman *et al.* 2005). Howard *et al.* (1996) found differences in moth species composition between different elevations in Kibale. Certain species were found only in the southern parts of the park at low elevations, and some only in the northern parts which are about 200 m higher in altitude. Other studies have as well found changes in community composition along an altitudinal gradient. Brehm *et al.* (2003) found significant species turnover of Geometridae along the altitudinal gradient ranging from 1040 to 2677 m asl in an Ecuadorian montane rain forest. Also in Papua New Guinea Lepidoptera assemblages feeding on four species of *Ficus* changed between tropical lowland (100 m asl) and highland (1800 m asl) (Novotny *et al.* 2005).

Temporal variation in community composition

The community composition of herbivorous insects changed markedly between sampling dates. We also found a statistically significant interaction between spatial and temporal variation, which means that temporal changes in faunal composition are not synchronized among sites on this relatively small local scale. This apparently indicates asynchronous seasonal patterns inside the study area. Temporal variation in insect communities has been studied even less than spatial variation (Grøtan *et al.* 2012, Novotny & Weiblen 2005, Valtonen *et al.* in press). Beetles belonging to the family Carabidae exhibited significant temporal species turnover in a 3-y study by Lucky *et al.* (2002). In a 1-y study in Ecuador, nymphalid butterflies also showed temporal variation in community structure (DeVries *et al.* 1997). In a 12-y study, A. Valtonen *et al.* (in press) found a seasonal pattern in the similarity of fruit-feeding butterfly assemblages in Kibale National Park. In the beginning of both rainy seasons communities became very similar but the two dry seasons sent the assemblages in different directions. Communities differed significantly among sampled years but annual changes in butterfly communities were unidirectional. Grøtan *et al.* (2012) found annual cycles in fruit-feeding butterfly community similarities in Ecuador, and also a gradual decline in similarities with increasing time lag. Therefore, it seems that tropical insect communities exhibit predictable within-year changes, while differences among years are far more unpredictable.

Species richness and abundance

Our study confirms a common observation in tropical insect research, that the species-accumulation curve does not reach an asymptote (Novotny & Basset 2000). The insect communities were strongly dominated by a few abundant species. The same kind of community pattern was found in Papua New Guinea (Novotny *et al.* 2002c). The dominant species Cecidomyiidae sp. 2 (the hard leaf gall), Microlepidoptera sp. 1 (the round miner) and Geometridae sp. 1 can be assumed to be specialists that use only *N. macrocalyx* as a host because geometrids are usually specialists, as are most leaf miners and gall inducers (Bairstow *et al.* 2010, Dalbem & Mendonça 2006, Holloway 1994, Lopez-Vaamonde *et al.* 2003).

Diversity indices showed only minor differences among sites, despite the fact that densities and faunal communities varied. The presence of one dominant species can greatly affect the value of Simpson's diversity index (Davies *et al.* 1997). Traditional diversity indices, like Simpson's diversity index and Berger–Parker dominance index, alone are not very useful for measuring the diversity of a given locality, because they do not consider changes in community composition (Horner-Devine *et al.* 2003, Summerville *et al.* 2003, Uehara-Prado *et al.* 2007). The variation in density and faunal communities of herbivorous insects can be caused by among-site differences in host plant density or quality, micro-environment, or abundance of natural enemies (Chapman *et al.* 1997, Denno *et al.* 2005, DeVries *et al.* 1997, Yamamoto *et al.* 2007).

We detected clear seasonal variation in the total abundance of insects, despite the fact that *N. macrocalyx* produces leaves throughout the year. Therefore, it is evident that food availability is not the main factor regulating the densities of insects associated with this tree species. The highest number of insects was collected in March and the lowest in November. Skippari *et al.* (2009) got exactly opposite results. They found the highest number of individuals in October–November and, like DeVries *et al.* (2012), found that precipitation had no effect on the

abundance of herbivorous insects. But Nummelin (1989) found that arthropod abundance in Kibale correlated with rainfall with a time lag of 1–3 mo. Valtonen *et al.* (in press) found that there is a 1-mo lag between the rainfall peak and the vegetation greenness peak, while butterfly abundance reaches its maximum 3 mo after the vegetation greenness peak. Therefore, they predicted highest butterfly abundances in February–March and August–September based on 12 y of data on fruit-feeding butterflies from Kibale National Park. The time lag could be explained by the development time of insect larvae into adults, which varies among species. During the dry months (June–August), herbivory, measured in percentage of leaf area eaten, on *N. macrocalyx* was much lower, which would suggest also lower insect abundance during the dry season (Kasenene & Roininen 1999). However in our study the insect abundance in July was quite high, but samples in July were dominated by Microlepidoptera sp. 1, which represented over 50% of the individuals. Also the high Berger–Parker dominance index shows the dominance of this species, which is a leaf miner and benefits if the level of folivory is low. Without Microlepidoptera sp. 1, July would have had the lowest abundance. Seasonal variation is common among tropical rain-forest insects (DeVries *et al.* 1997, Wolda 1992). Therefore, the well-known fluctuation in precipitation and changes in the timing of rainy seasons in Kibale National Park might cause the irregular variation in insect abundances (Struhsaker 1997). Our results and previous studies suggest that 1 y of sampling is not sufficient to fully detect the variation in insect abundance in this area.

We also found temporal variation in species richness. The fewest species were collected in November, while the number of species peaked during the rainy season in March. Savilaakso (2009) detected that species richness of Lepidoptera larvae correlated positively with monthly precipitation, which would explain the high species richness in March, but not the low number of species in November. In Ecuador, Grøtan *et al.* (2012) found highest butterfly diversity during the dry season and lowest during the wet season. Also Valtonen *et al.* (in press) predicted highest species richness for butterflies during dry seasons. Both studies found a time lag of 2 mo between the peak in rainfall and maximum species richness. Also in other studies, rainfall has been found to affect the number of insect species collected (Bairstow *et al.* 2010, DeVries *et al.* 2012).

Conclusions

The observed spatial variation in community composition of herbivorous insects feeding on *N. macrocalyx* in Kibale National Park is most likely caused by differences in vegetation, altitude and microclimate among the study sites. The temporal variation in herbivore assemblages is probably caused by seasonal changes in climate and the phenology of other host plants used by generalist herbivore species. These environmental differences may have a great influence on the herbivorous insect species, which are dependent on their host plants and climate. To better understand the global patterns of spatial and temporal variation in community composition, more studies are evidently needed in tropical rain forests.

Globally, the most important reason for species extinction is the destruction of their natural habitats (Pimm & Raven 2000). If spatial species turnover is low, communities do not suffer as much from habitat loss as when turnover is high (Fonseca 2009). Thus, when biodiversity is evaluated or studied in Afrotropical rain forests, it is important to take into consideration that spatial and temporal variation of community composition can be high. The reliable diversity of an area can be measured only if the faunal composition has been monitored during a long period of time from many sites. As our study shows, compositional turnover can be surprisingly high even across relatively small distances.

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Appendix 1. List of the insect species and their abundances at each study site. Morphospecies for which generic and familial assignments were confirmed by DNA barcoding and the BOLD database are indicated by asterisks.

	Sebitoli	Compart. K30	Mpanga River	Machwamba River	Ngogo	Dura River	Mainaro
Lepidoptera							
Geometridae							
Geometridae sp. 1*	790	370	98	263	414	140	60
Geometridae sp. 6	0	0	0	0	0	0	1
Geometridae sp. 7*	16	6	2	5	2	2	0
Geometridae sp. 8*	21	11	2	7	0	0	0
Geometridae sp. 12*	0	1	0	3	2	1	0
Geometridae sp. 15*	1	1	1	0	0	1	0
Geometridae sp. 17*	20	6	3	8	7	3	10
Geometridae sp. 22*	3	2	0	1	2	2	0
Geometridae sp. 31*	0	1	1	0	0	1	1
Geometridae sp. 35*	0	0	1	0	0	0	0
Geometridae sp. 34	0	0	1	0	0	0	0
Geometridae sp. 51*	1	0	0	0	2	1	0
Cleora sp. 1*	0	0	0	0	0	1	0
Cleora sp. 2*	1	1	1	2	1	0	1
Cleora herbuloti Fletcher*	3	1	1	0	0	0	0
Prasinocyma sp. 1*	3	1	2	2	1	3	2
Prasinocyma sp. 2*	1	0	0	0	0	0	0
Scopula sp.*	1	2	0	0	0	0	0
Oedicentra sp.*	1	0	1	0	1	1	0
Chloroclystis sp.*	0	1	0	0	0	0	0
Nolidae							
Nolidae sp. 4*	13	11	10	15	5	10	6
Nolidae sp. 5*	1	0	0	0	0	0	0
Nola sp. 1*	6	14	5	7	0	0	1
Erebidae							
Erebidae sp. 1	8	28	9	10	13	7	4
Erebidae sp. 2	17	37	12	18	16	6	7
Erebidae sp. 4*	0	0	0	0	0	0	14
Erebidae sp. 7*	14	9	1	1	0	0	1
Erebidae sp. 8	0	1	0	1	0	0	0
Erebidae sp. 10	0	0	0	1	1	0	0
Erebidae sp. 11*	7	0	0	0	0	0	0
Erebidae sp. 12	0	15	0	0	0	0	0
Erebidae sp. 14	6	0	0	0	0	0	0
Erebidae sp. 15	0	21	0	0	0	0	0
Erebidae sp. 16	0	0	1	0	0	0	1
Erebidae sp. 17	0	0	0	0	1	0	0
Noctuidae							
Noctuidae sp.20	0	0	1	1	0	2	0
Noctuidae sp.65	0	0	0	0	0	0	1
Noctuidae sp.68	0	0	0	0	0	0	1
Noctuidae sp.70*	2	1	1	0	3	6	107
Noctuidae sp.71*	11	9	12	3	3	7	9
Noctuidae sp. 72*	0	0	0	1	0	0	0
Tortricidae							
Tortricidae sp. 1*	29	16	4	9	3	3	0
Tortricidae sp. 2*	6	3	3	10	0	4	1
Gelechiidae							
Gelechiidae sp. 9	2	1	0	1	1	3	1
Crambidae							
Crambidae sp.*	0	2	0	0	1	1	0
Lasiocampidae							
Lasiocampidae sp. 2	1	0	0	0	0	0	0
Stoermeriana sp.*	0	0	1	0	0	0	4
Limacodidae							
Limacodidae sp. 1	0	0	1	0	0	0	0
Limacodidae sp. 2	4	0	0	1	0	0	0

Appendix 1. Continued.

	Sebitoli	Compart. K30	Mpanga River	Machwamba River	Ngogo	Dura River	Mainaro
Nymphalidae							
Acraea sp.*	0	0	0	0	1	0	0
Nymphalidae sp. 4	0	0	0	1	1	0	0
Charaxes sp. 1	0	1	0	0	0	0	1
Bombycoidea							
Bombycoidea sp. 1	0	0	1	0	0	0	0
Microlepidoptera							
Microlepidoptera sp. 1	843	940	42	706	750	408	328
Microlepidoptera sp. 2	7	3	1	5	17	10	0
Diptera							
Cecidomyiidae							
Cecidomyiidae sp. 1	15	37	13	20	6	2	93
Cecidomyiidae sp. 2	602	973	1892	1449	52	308	221
Cecidomyiidae sp. 3	77	15	6	39	4	20	12
Cecidomyiidae sp. 4	1	54	0	33	0	0	0
Cecidomyiidae sp. 5	5	7	0	5	4	0	0
Cecidomyiidae sp. 6	0	2	0	0	0	0	0
Hemiptera							
Psyllidae							
Psyllidae sp. 1	31	53	7	148	3	3	199
Coleoptera							
Curculionidae							
Curculionidae sp. 1 (adult)	28	13	72	125	67	59	160

Appendix 2. List of tree species and their basal areas (m^2 ha^{-1}) found from each study site. Nomenclature follows Hamilton (1991) and Kalema & Beentje (2012).

	Sebitoli	Compart. K30	Mpanga River	Machwamba River	Ngogo	Dura River	Mainaro
Arecaceae							
Phoenix reclinata	0	0	0.22	0	0	0	0.27
Capparaceae							
Euadenia eminens	0.04	0.10	0	0	0	0	0
Celastraceae							
Cassine buchananii	0	0	0	0	0.56	0	0
Cassine aethiopica	0	0	0.88	0	0	0	0.51
Sapotaceae							
Chrysophyllum sp.	0.47	0.32	0	0	3.63	1.96	1.68
Mimusops bagshawei	0.65	1.09	0	0	0.02	0.69	0.16
Aningeria altissima	0.14	0	0.06	0	0	7.55	0
Bequaertiodendron oblanceolatum	0	0	0	0	0	3.36	0.18
Ebenaceae							
Diospyros abyssinica	0	0.19	1.30	0.91	0.17	0	0
Fabaceae							
Albizia grandibracteata	0	0	1.08	0	0	0	0.14
Erythrina abyssinica	0	0	0	0.03	0	0	0
Newtonia buchananii	2.05	0.08	0	0	22.78	0	0
Cynometra alexandri	0	0	0	0	0	0.26	31.56
Millettia dura	0	0.17	0.03	1.02	1.03	0	0
Apocynaceae							
Funtumia africana	0.83	1.47	4.41	1.68	1.70	0.70	0
Pleiocarpa pycnantha	0.03	0.03	0	0	0	0	0
Rauvolfia vomitoria	0	0	0	0	0.28	0	0
Conopharyngia spp.	0	0.37	0.06	0	0.05	0	0
Rubiaceae							
Tarenna pavettoides	0	0.09	0	0	0.04	0	0
Mitragyna stipulosa	0	0.41	0	0.19	0	0	0
Rothmannia urcelliformis	0	0	0	0.02	0	0	0.12
Melianthaceae							
Bersama abyssinica	0	0.13	0	0	0	0	0

Appendix 2. Continued.

	Sebitoli	Compart. K30	Mpanga River	Machwamba River	Ngogo	Dura River	Mainaro
Oleaceae							
Linociera johnsonii	0	0	0	0	1.90	0.02	0
Bignoniaceae							
Markhamia platycalyx	0	6.35	0.34	0.88	0.85	0.03	0.02
Verbenaceae							
Premna angolensis	0.25	0	1.61	1.99	0.46	0	0
Monimiaceae							
Xymalos monospora	0.05	0	0.04	0	0.05	0	0
Achariaceae							
Dasylepis spp.	0.03	0	0	0	0.08	0	0
Phyllanthaceae							
Bridelia micrantha	0	0	0.55	0	0	0	0
Euphorbiaceae							
Croton megalocarpus	5.48	0.36	0.67	0	0	0	0
Neoboutonia macrocalyx	0.74	0.74	0.54	0.79	0.29	0	0
Sapium ellipticum	0	0	0	0.19	0	0	0
Salicaceae							
Casearia battiscombei	0	0.05	0.62	0.41	0.19	0.02	0
Clusiaceae (Guttiferae)							
Symphonia globulifera	0	6.28	0	0	0	0	0
Sterculiaceae							
Leptonychia mildbraedii	0.07	0.06	0	0	0	0	0.04
Pterygota mildbraedii	0	0	0	0	33.73	0.40	0
Annonaceae							
Monodora myristica	0	1.92	0	0	1.37	3.84	0
Uvariopsis congensis	0.04	0	0	0	1.37	0.73	0.21
Oleaceae							
Olea welwitschii	0	0	0	0.15	0.80	0	0
Oliniceae							
Olinia rochetiana	0	0	0	0.07	0	0	0
Rhizophoraceae							
Cassipourea ruwensorensis	0	0.03	0	0	0.12	0	0
Cannabaceae							
Celtis africana	0.20	0	0	0	0.21	0	0
Celtis durandii	2.06	2.02	0.12	2.17	1.31	4.03	0.87
Ulmaceae							
Chaetacme aristata	0.82	0	1.89	0.03	0	0	0
Moraceae							
Trilepisium madagascariensis	1.80	2.07	0.32	0.38	0.62	0	0
Ficus exasperata	0	5.52	0	0.21	0	0	0
Ficus natalensis	4.08	0	0	0	0	0	0
Ficus sansibarica	19.51	0	0	0	0	1.69	0
Ficus saussureana	0.60	0	0.89	0	0	9.76	0
Ficus sur	2.61	0	0	0	0	0	0
Ficus valis-choudae	0.11	0	0	0	0	0	0.34
Myrianthus holstii	0.24	0.37	0	0	0	0	0
Rosaceae							
Prunus africana	0.63	0	0.16	0.04	0.37	0	0
Rhamnaceae							
Maesopsis eminii	0.05	0	0	0	0	0	0
Rutaceae							
Clausena anisata	0	0	0	0.02	0	0	0
Fagaropsis angolensis	0.75	0	1.38	0.03	0.24	0	0
Teclea nobilis	0.07	0.73	0	0	0.16	0	0
Zanthoxylum leprieurii	0	0	0	0.16	0	0	0
Meliaceae							
Lovoa trichilioides	0	0	0	0.10	0	0	0
Carapa grandiflora	0.29	0	0	0	0	0	0

Appendix 2. Continued.

	Sebitoli	Compart. K30	Mpanga River	Machwamba River	Ngogo	Dura River	Mainaro
Anacardiaceae							
Pseudospondias microcarpa	0.29	0.10	15.24	17.29	0.21	15.98	8.94
Sapindaceae							
Pancovia turbinata	0.20	0	0	0	0	0	0
Blighia unijugata	1	0.40	5.01	0	0	0	0
Aphania senegalensis	0	0	0.24	0	0.09	0	0
Olacaceae							
Strombosia scheffleri	2.25	10.56	0	3.05	0	0.30	0
Bignoniaceae							
Kigelia africana	0	0.06	0	0.06	0.04	0	0
Zygophyllaceae							
Balanites wilsoniana	0	0.02	2.30	0	0	3.21	0
Boraginaceae							
Cordia abyssinica	1.00	0.03	0.59	0	0	0	0
Cordia millenii	0.12	0	0	0	0	0	0
Unidentified 1	0	0	0	0	0.16	0.02	0
Unidentified 2	0	0	0	0	0	0	0.49
Total	49.54	42.11	40.53	31.86	74.90	54.58	45.54